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Filling-in the details on perceptual fading

Andrew E. Welchman *, Julie M. Harris

Neural Systems Group, Department of Psychology, Ridley Building, University of Newcastle-upon-Tyne, Newcastle-upon-Tyne, NE1 7RU, UK

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Abstract

We examined the perceptual disappearance (or 'filling in') of a peripheral target surrounded by dynamic texture. Targets defined by different visual attributes were used to explore the importance of target properties in determining the time-course of fading. Introducing luminance-, motion- or direction-contrast between the target and background increased the time-to-fade. For motion contrast, this was related to target visibility. Targets defined by a difference of texture from the background took longer to fade than those defined by a difference of motion. This might correspond to activity in different visual areas, or could be due to different visibilities in each case. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Filling-in; Texture; Motion; Contrast; Adaptation

1. Introduction

Despite very poor visual acuity outside the central 2 degrees of vision, we have a compelling perception of a whole, detailed world. How does the brain process the visual properties of the world to produce this subjective perception of a detailed representation? This question has been addressed by many vision scientists and philosophers of mind, and is clearly moot (Teller, 1984; Dennett, 1991; O'Regan, 1992; Churchland & Ramachandran, 1993; Pessoa, Thompson, & Noë, 1998).

Recent insights into the brain's strategies for representing the world have come from considering a range of perceptual phenomena where the brain is described as 'filling-in' information about the world that the retina is not able to encode. For example, there is perceptual completion across the retinal blind spot (Sergent, 1988; Ramachandran, 1992; Murakami, 1995; Tripathy, Levi, Ogmen, & Harden, 1995) and across retinal lesions (Murakami, Komatsu, & Kinoshita, 1997). Also, images stabilised on the retina will perceptually fade to be replaced by non-stabilised information that surrounds them (Krauskopf, 1963; Gerrits, De-Haan, & Vendrik, 1966). Further, work examining surface perception has suggested that features, such as brightness, are propagated within object boundaries at a finite rate (Paradiso & Nakayama, 1991; Davey, Maddess, & Srinivasan, 1998). This has been taken as suggestive of a role for an active process of neuronal filling-in in normal surface perception (Walls, 1954; Cohen & Grossberg 1984; Arrington, 1994).

A number of studies have reported the perceptual disappearance of a target item when presented for several seconds within a field of dynamic random texture (e.g. Anstis, 1989; Ramachandran & Gregory, 1991; Spillmann & Kurtenbach, 1992; Hardage & Tyler, 1995; De Weerd, Desimone, & Ungerleider, 1998). In all these studies, the textured background pattern is rapidly refreshed, ensuring that the perceptual illusion cannot simply reflect low-level adaptation; rather, it must be explained at least in terms of the extraction of the second-order characteristics (such as texture contrast) of the scene. Anstis, and later Ramachandran and Gregory, noticed the similarity between this illusion and that experienced around retinal scotomata; Ramachandran and Gregory thus describe the experimental set-up as inducing an 'artificial scotoma'.

This perceptual illusion raises a number of interesting questions. First, why do things fade and what does this tell us about how basic visual processes combine to result in a stable percept of the world? For instance, how does information from the outside world interact

* Corresponding author. Fax: +44-1912-225622.
E-mail address: a.e.welchman@ncl.ac.uk (A.E. Welchman).

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with brain activity: does the 'filled-in' percept after twelve seconds of adaptation reflect the neural activity early in the visual cortex? Alternatively, might higher cortical areas 'hypothesise' about the structure of the visual scene, ignoring areas that remain unchanged for 12 s as aberrations or visual noise?

Another set of issues concerns how the visual system responds to the target area once the target is no longer subjectively present. What are its properties? How might they relate to the processes occurring during the adaptation period? In this paper, we focus on the question of adaptation. What determines how long it takes for perceptual fading[1] of a target to occur? What might this imply about the underlying neural activity? Specifically, we will consider the physical properties of the target and the ways they affect the time course of the adaptation process.

Recently De Weerd et al. (1998) suggested that neural competition between the representation of the target and that of the surround is responsible for the phenomenon of fading. They argued that on initial viewing of the stimulus a strong boundary representation is formed between the target and the surrounding dots that allows the areas to be segmented. They suggested that once adaptation of the target-surround boundary occurs, the antagonistic processes that keep the two representations separate fails, allowing the neural propagation of the dominant representation. They argued that this usually results in the surrounding texture invading the target to produce the 'filled in' percept. This is a compelling suggestion, but one that has not yet been empirically tested.

Indeed, very little work has addressed the processes involved in the adaptation of the target or the nature of the competition between the target and the surround. Here, we begin to address these issues by considering how perceptual fading is affected by the physical properties of the target.

In addition, considering target properties enforces a semantic point. Labelling the illusion an 'artificial scotoma' has lead to the importance of target attributes being somewhat ignored, with descriptions of the visual stimuli simply referring to the target as a 'hole' in the texture (De Weerd, Gattass, Desimone, & Ungerleider, 1995; Pessoa et al., 1998). If, as the term 'scotoma' suggests, the target is treated like a hole after adaptation has occurred, the results of this paper should make clear that it is not treated as such beforehand. We explore perceptual fading using stimuli in which the visual attributes of both the target and background can differ. We examine how a target's luminance or motion affects its time-to-fade, measure the relationship between time-to-fade and visibility, and make a comparison between targets whose properties differ.

2. Methods

2.1. Stimuli

An IBM compatible PC containing a #9 Revolution 3D graphics card generated the stimuli. Stimuli were presented on a luminance-calibrated Nanao T2-17 monitor at a distance of 50 cm from the subject, whose head was steadied on a chin rest. The screen area subtended 30×24 deg, and individual dots subtended 0.11 deg^2. The experimental stimulus consisted of a target, the background containing dynamic random noise and a red fixation cross. We describe experiments using two types of target: (i) a difference of texture (DOT) target, consisting of a uniform grey square (51.6 cd m^{-2}) on a dynamic random dot background (note that for this condition there is actually a difference of both texture and motion); and (ii) a difference of motion (DOM) target, consisting of a square containing a random pattern of black and white dots that were stationary or moved coherently with a velocity of 2.2 deg s^{-1}, on a dynamic random dot background. (See Fig. 1B.) The background consisted of 50% white (101.5 cd m^{-2}) dots on a dark background (1.7 cd m^{-2}). The position of individual white dots was randomly assigned on the screen 20 times per second. Spillmann and Kurtenbach (1992) note that such rates of re-assignment facilitate perceptual fading. The dynamic random noise had a mean luminance of 51.6 cd m^{-2}.

2.2. Procedure

Subjects were instructed to maintain fixation at the fixation cross. They depressed a button on a hand-held response box to initiate stimulus presentation. They held down the button until the target was no longer visible.

After releasing the button, they were presented with a masking pattern consisting of 0.22×0.22 deg squares (separated by 0.22 deg) on a black background. Each square's luminance alternated between light grey (80 cd m^{-2}) and dark grey (36 cd m^{-2}) every 450 ms. The dark and light squares were spatially alternated across the screen. The mask screen reduced the perceptual aftereffects previously reported with this stimulus (Ramachandran & Gregory, 1991; Hardage & Tyler, 1995).

[1] A point about our terminology. Previous studies have variously described the phenomenological percept under this experimental paradigm as 'perceptual filling-in' (Ramachandran & Gregory, 1991; De Weerd et al., 1998) or 'perceptual fading' (Spillmann & Kurtenbach, 1992; Ramachandran, Gregory, & Aiken, 1993). Given the debate about the relationship between perceptual filling-in and neuronal filling-in (see Pessoa et al. (1998)), we adopt the more neutral term 'perceptual fading' and refer to the time taken for the target to disappear as the 'time-to-fade'.

After 2 s subjects could initiate a new trial on which the target was presented at the same location. The temporal sequence is shown in Fig. 2.

The time taken for the target to fade from view was measured on each trial. Each subject made 30 responses during an experimental run: five of these were catch trials in which the target was gradually replaced by random noise. The mean time-to-fade was calculated from the other 25 trials. Subjects occasionally released the response button unintentionally (ca. 1% of trials), generally doing so soon after the initiation of the trial: for this reason, response times below 1 second were removed from the analysis. Catch trial data were inspected to ensure that subjects adhered to the task, but were not analysed further.

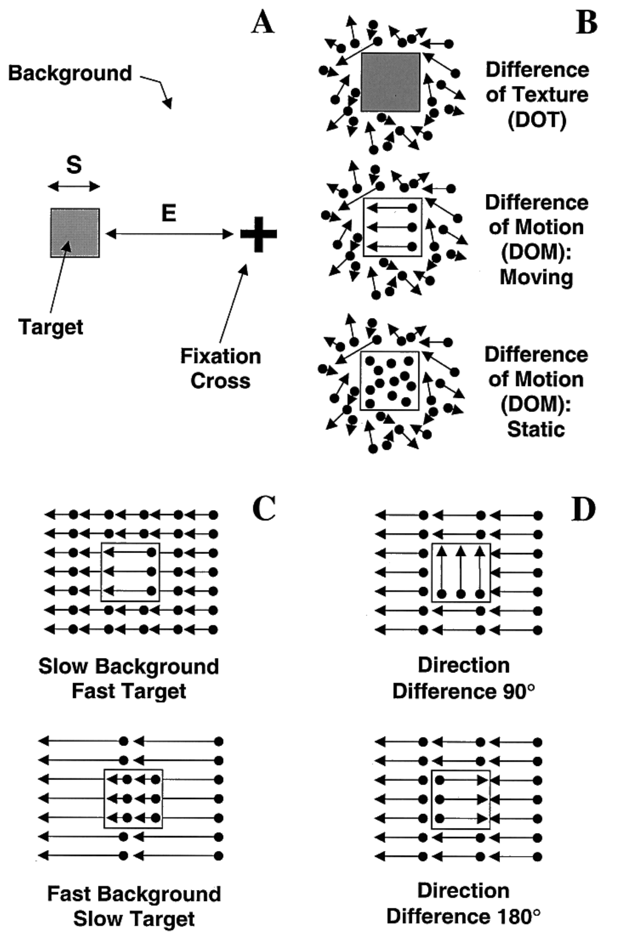

Fig. 1. Cartoon representations of the stimulus configuration. (A) Spatial arrangement of the stimulus. For experiment 3, target eccentricity was varied by changing the distance E. Target size was varied by changing the side length S. (B) Representations of the local area around the target. Dynamic random noise surrounds a target that is defined either by a difference of texture (DOT), or by a difference of motion (DOM). The random noise background contains motions in all directions and with all speeds. DOM targets contained a random pattern of black and white dots that either moved coherently with a constant speed (middle panel) or were static (bottom panel). (C, D) Representations of the local area around the target used in experiment 2. The speed of dots in the background and those in the target were varied (C); the direction of the target dots was varied (D).

2.3. Subjects

Three experienced observers were principally used in the experiments: two were the authors whilst the other was naïve about the aims of the experiment. Inexperienced naïve subjects (undergraduates participating for course credit) were also used to obtain selective data. The inexperienced subjects responded in similar ways to the three principal observers; their data are not presented. All had normal (or corrected to normal) vision.

3. Results

3.1. Experiment 1

This experiment set out to test how the physical attributes of the target affect the time-to-fade. This was done using the stimulus studied in the previous work on the illusion. We made a simple manipulation: changing the luminance of a DOT target that was surrounded by dynamic random noise.

Target luminance was varied from 1.7 to 101.5 cd m^{-2}. The mean luminance of the background fixed at 51.6 cd m^{-2}. The stimulus configuration is shown in Fig. 1A. The target, 1.5×1.5 deg in size, was presented 10 deg from the fixation cross. For subjects JSM and JMH the data for each luminance value were collected in separate experimental runs. Subject AEW performed a longer experiment in which different target luminances were randomly interspersed on the same run. Fig. 3 shows the data. The luminance of the target relative to the background is plotted against normalised time-to-fade. The normalised time-to-fade expresses time-to-fade values as a percentage of that obtained at mean luminance (i.e. 100% = time-to-fade at mean luminance).

The data from subjects AEW and JMH suggest a U-shaped function around the value of mean luminance, whilst JSM's data suggest a W-shaped function, but also with a dip around mean luminance. As the luminance of the target is moved away from mean background luminance time-to-fade increases. It is noteworthy that the minimum of the time-to-fade plots corresponds closely to the mean luminance of the background texture. This suggests that deviation away from the mean (i.e. the introduction of luminance contrast between the target and background) causes an increase in the time-to-fade.[2]

[2] A control experiment showed that the contrast between the target and the background, rather than luminance, determines the shape of the time-to-fade function. Varying the luminance of the target, whilst ensuring it still had the mean luminance of the surrounding texture, produced little change in the time-to-fade.

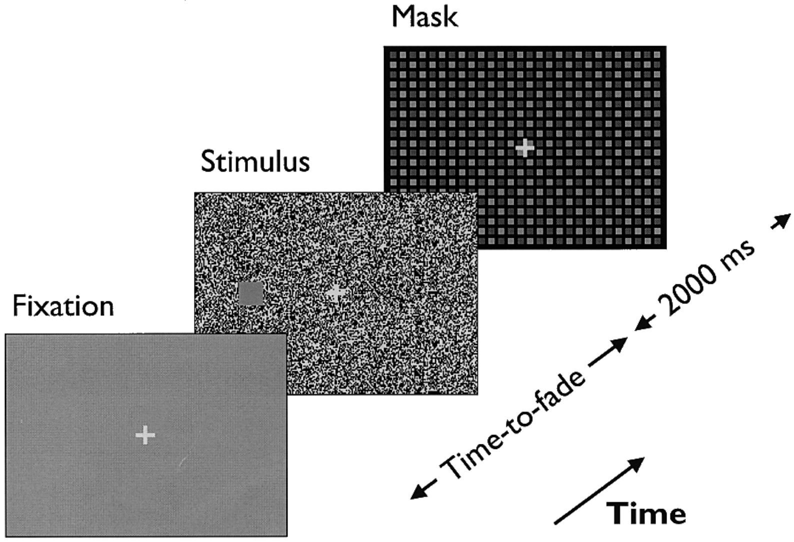

Fig. 2. A representation of the temporal sequence of the experiment. Subjects pressed a button to initiate presentation of the stimulus. They kept the button held down until the target (shown here as a grey square) had faded from view. After releasing the button, they were presented with the masking screen for 2 s to reduce any after effects from viewing the stimulus. The fixation screen was then presented.

Clearly, perceptual fading does not occur solely because the target is static on a dynamic background, or because there is a difference in texture between the target and its surround. Other features of the target must also adapt before perceptual fading can occur.

These data might also provide some insight into the suggested importance of the target-surround boundary (De Weerd et al., 1998). Manipulating target luminance should have little effect on the boundary strength in a local area. As the target's luminance is increased, its contrast with the black dots in the background will also increase; however, the target's contrast with the white dots will decrease. The net result of such changes, even given a small anisotropy in the perception of luminance, would be fairly equivocal, predicting a flat function with time-to-fade. This was not found. The data make more sense if the differences between the target and surround are considered in more spatially extensive terms. If local luminance values are averaged across a spatially extended region, then the difference between target luminance and average background luminance would be expected to influence time-to-fade. This is what we observed. This spatial averaging of luminance information could be achieved through low pass filtering of the visual input: note that the targets were presented at an eccentricity of 10 deg.

Whilst the three observers produce broadly similar results, there is an intriguing dip in AEW's data at the lowest luminance level, with the time-to-fade returning to the baseline value that is provided by a mean luminance target. Subject JMH also reported perceiving a different type of fading at the lowest target luminance,

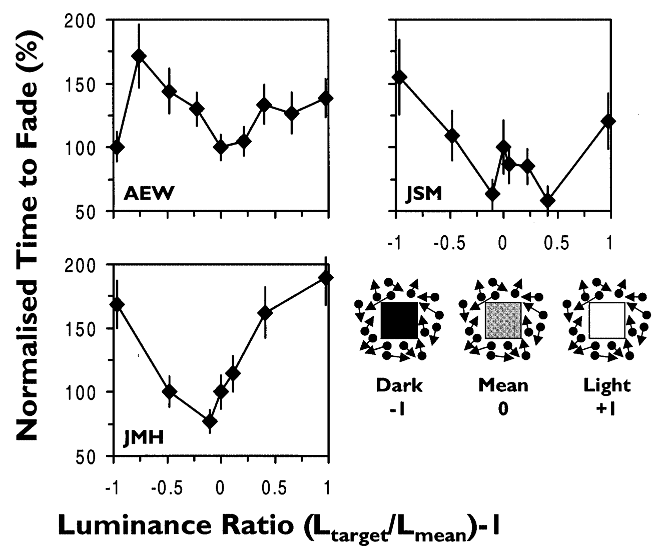

Fig. 3. Time-to-fade plots for three subjects showing the effects of changing the luminance of a DOT target. The abscissa shows the luminance of the target relative to the background. A value of -1 corresponds to a dark target (1.7 cd m^{-2}); a value of 1 corresponds to a light target (101.5 cd m^{-2}); 0 corresponds to the mean luminance of the background texture. The ordinate presents the time-to-fade data normalised to the value obtained for a target of mean luminance, expressed as a percentage. A value of 100 corresponds to that obtained at mean luminance. Values above 100 correspond to times longer than obtained at mean luminance, whilst values below 100 correspond to shorter times. The times-to-fade for mean luminance differed between subjects (AEW = 17. s; JSM = 28.8 s; JMH = 14.8 s). Error bars represent the S.E.s of the mean standardised to the baseline value provided by the time-to-fade for mean luminance (see Taylor (1997) for details).

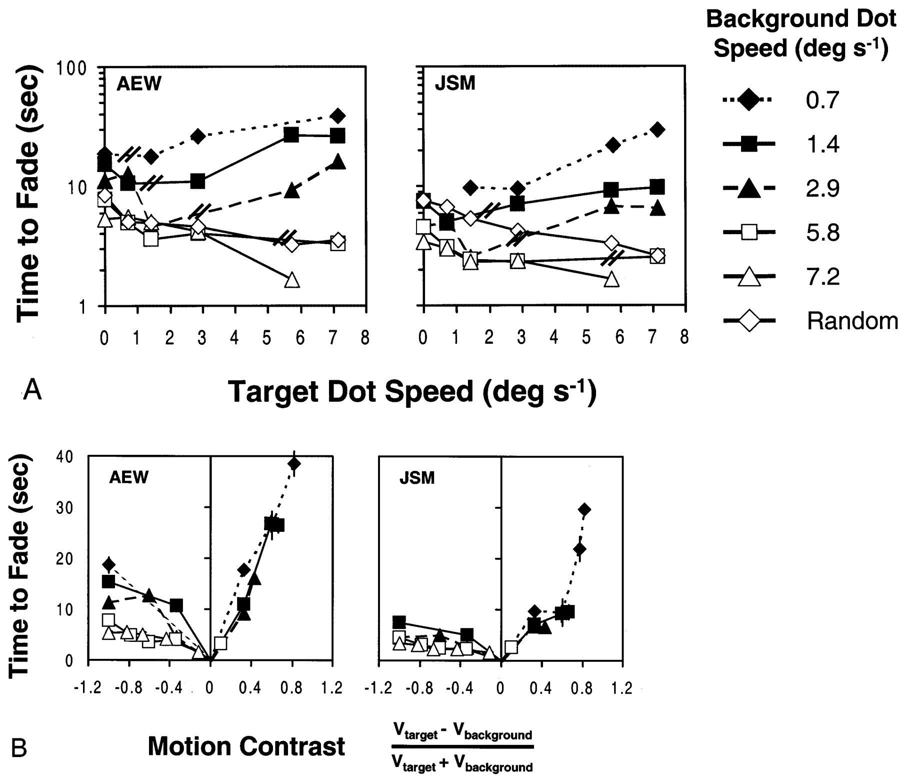

Fig. 4. Time-to-fade plots for different speeds of motion in the target area and the background. (A) Time-to-fade plots as a function of the speed of the dots within the target. Each curve represents the data obtained for a different speed of background dot movement. Filled symbols represent slow background speeds, whilst open symbols represent faster speeds. The data for targets surrounded by incoherent dynamic random noise is shown by open diamonds. Note that the ordinate is a logarithmic scale for clarity of presentation. When the target dot speed equals the background dot speed, time-to-fade will be zero by definition. The data points for each series are connected to assist visual inspection — however a double dash symbol (//) is shown to indicate the point where target dot speed equals background dot speed (i.e. time-to-fade = 0). Error bars, representing the S.E. of the mean time-to-fade, are plotted: most lie within the symbols, and so are not visible. (B) The data from Fig. 4A re-plotted as a function of the motion contrast of the dots in the target and the surround. Motion contrast is defined as $(V_{\text{target}} - V_{\text{background}})/(V_{\text{target}} + V_{\text{background}})$, where V_{target} is the speed of the dots in the target, and $V_{\text{background}}$ the speed of dots in the background. As in Fig. 4A, each curve represents a different background speed. Again, error bars are plotted, but are not always visible.

although no reduction in time-to-fade was observed. It is possible that a different process was in action at the lowest luminance values. The associated change in the subjective perception might have been treated differently by the three subjects.

3.2. Experiment 2

The first experiment established that the difference between the physical properties of the target and its surround is important in determining time-to-fade. In this section we focus on understanding this difference in more detail. To do this we adopted a new stimulus configuration. We used a difference of motion (DOM) stimulus (see Fig. 1B) in which, the background, as well as the target, contained a coherently moving random dot pattern. This enabled us to examine the velocity of the target dots relative to the background dots (see Fig. 1C and D). This stimulus has a major advantage over the configurations previously examined as the target is defined by its difference from the background along only one visual dimension. This allows a simpler understanding of the relationship between target and background than placing a grey, texture-less square in dynamic random noise. We examined how differences in motion (speed and direction) between target and background affected time-to-fade.

3.2.1. The effects of speed of motion

The speed of the dots in the background was varied from 0.7 to 7.2 deg s^{-1} and times-to-fade recorded for targets containing dots moving at a speed between 0.7 and 7.2 deg s^{-1}. The 1.5×1.5 deg target was located at 10 deg eccentricity. The speeds in the target and background were fixed on an experimental run. The data are presented in Fig. 4.

The results of this experiment show that the mechanisms responsible for perceptual fading are sensitive to motion contrast. Fig. 4A presents time-to-fade as a function of the speed of motion in the target. Each curve shows the time-to-fade function for a different background speed. By considering a vertical slice

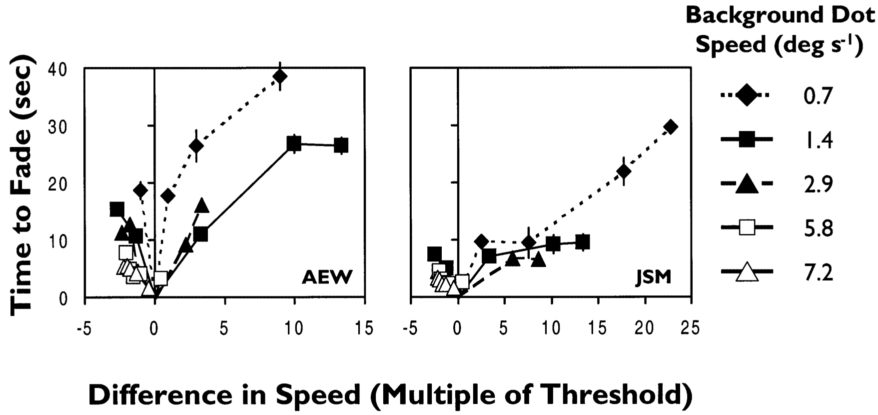

Fig. 5. Time-to-fade plotted as a function of target visibility. Time-to-fade plots as a function of the difference in speed between target and background dots, expressed as a multiple of detection threshold. Each curve represents the data obtained for a different background speed. Thresholds for detecting the presence of the target were obtained separately for each background speed. The difference between the target dot speed and the background dot speed used to obtain the time-to-fade was then expressed as a multiple of detection threshold. Error bars, representing the S.E. of the mean time-to-fade, are plotted but most lie within the symbols.

through the data, it can be seen that slow-moving backgrounds (filled symbols) make perceptual fading harder (indeed, fading is very difficult to achieve at all if the background is static). As the velocity of the background dots increases, perceptual fading of the target occurs faster (open symbols). By considering the data grouped by background speed (i.e. one curve on Fig. 4A at a time), it can be observed that for slow-moving backgrounds (filled symbols), as the speed of the dots in the target patch increases so time-to-fade increases quite dramatically (note that the ordinate has a logarithmic scale). However, for faster background dot speeds (open symbols) there is a decrease in the time-to-fade as the speed of the target dots increases. This suggests that the contrast between the background speed and the target speed is important in determining time-to-fade.

To clarify this point, the time-to-fade data are re-plotted in Fig. 4B as a function of the motion contrast between the target and background. Each series in Fig. 4B represents a different background speed. The figure clearly demonstrates that reducing motion contrast leads to a reduction in the time-to-fade. However, the effect is not symmetrical: the slower background speeds (filled symbols) produce longer times-to-fade than do the faster background speeds (open symbols). Also, longer times-to-fade are produced when the target moves faster than the background (right-hand side of the graph) than when the target moves slower than the background (left-hand side of the graph). Why might this be so? The effects might be due to changes in target visibility at different background speeds. If the target were more visible at slower background speeds then this may prolong the time-to-fade. To test this notion, we obtained thresholds for the detection of targets containing different speeds of motion from their surrounds.

3.2.2. Relating time-to-fade to target visibility

Targets, containing coherently moving dots, were presented on a background of moving dots. We manipulated the dot speed in the target and background separately, over the ranges used in Section 3.2.1. Subjects were required to detect the presence of the target. Thresholds were obtained using the method of constant stimuli under a two-interval forced choice procedure. One interval contained target dots moving at a different speed from those in the background, whilst the other contained target dots moving at the same speed as the background dots. Stimulus intervals lasted 500 ms and were separated by 250 ms. Detection thresholds for target dots moving faster than the background dots were measured separately from target dots that moved slower than background dots. Thresholds were approximately Weberian with mean Weber fractions of 0.500 for AEW and 0.400 for JSM. Threshold values (not reported) were used in the analysis below.

Fig. 5 shows the time-to-fade data from Fig. 4 re-plotted as a function of target visibility. Visibility is expressed as the difference between the speed of target and background dots in terms of multiples of detection threshold. Positive differences indicate target dot speed was faster than background dot speed, whilst negative differences indicate target dot speed was slower. The first point to note is that, as detection thresholds for slow background speeds are low, the targets presented on slow moving backgrounds were approximately 10–20 times above detection threshold. Conversely, as detection thresholds for fast background speeds are high, targets presented on fast moving backgrounds were a maximum of 2.5 times above threshold. The multiple of threshold appears to relate monotonically to the time-to-fade, with larger multiples of threshold corresponding to longer fading times. However, detection multiple does not uniquely determine fading time — the different series on Fig. 5 have different gradients, and there is a pattern of vertical ordering of the series. This suggests that the speed of background dot movement plays an important role in determining the time-to-fade. Whilst sensitivity to the motion contrast between the target and its surround is clearly important, the process of perceptual fading cannot be understood solely as a function of target detectability. It appears that the temporal energy of the background introduces an important non-linearity that plays a role in determining time-to-fade.

3.2.3. The effects of the direction of motion

Here we varied the relative direction of the dot motion in the target and the background. The experimental set-up was identical to that described in Section 3.2.1 except that the speed of the background and target were both 3.6 deg s^{-1} whilst the direction was varied (see Fig. 1D). Different directions were interleaved on the same experimental run. The results are presented in Fig. 6. Time-to-fade is shown as a function of the angular difference in motion direction between target and background dots.

The data show a high degree of directional tuning. Target dots travelling in a direction that is similar to the background dots (37 or 323 deg) fade quickly, whilst those travelling in the opposite direction to the background dots (180 deg) take longest to fade from view. The angular difference between target and background clearly appears to be important in determining the time-to-fade.

In summary, a clear message from experiment 2 is that, as we observed for luminance, increasing the contrast across a visual dimension (speed or direction) results in longer times-to-fade. The experiment also provided an insight into the role of the background dots in determining the time-to-fade. The stimulus was set up to define the difference between the target and surround along the same visual dimension. This allowed us to express differences between the target and surround in perceptual units of detection. Initial target visibility is important in determining time-to-fade, however, it is not uniquely important. Backgrounds with low temporal energy appear to prolong the time needed before perceptual fading occurs.

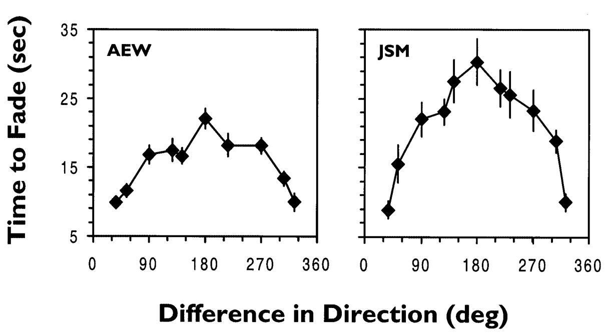

Fig. 6. Time-to-fade plots as a function of the angular difference in direction between the target dot direction and the background dot direction. The speed of each was constant at 3.6 deg s^{-1}. Error bars represent the S.E. of the mean time-to-fade.

3.3. Experiment 3

Having examined how the properties of the target and background interact to produce fading, in experiment 3 we compared times-to-fade for different types of target. We wanted to test how manipulating the target size and eccentricity would affect fading for different types of target. Previous research has found that perceptual fading is faster as the eccentricity of the target is increased and as the size of the target is reduced (Ramachandran et al., 1993; De Weerd et al., 1998). Here we compared the fading of DOT and DOM targets as size and eccentricity was varied. The difference of motion targets (see Fig. 1B) contained random dot pattern that was either static or moved coherently at 2.2 deg s^{-1} The difference of texture (DOT) targets were grey and texture-less. Their luminance was equal to the mean of the background dots. For all conditions, the background dots 'twinkled' incoherently.

3.3.1. Effects of eccentricity

A 1.5×1.5 deg target was presented at eccentricities ranging from 3 to 14 deg. The eccentricity of the target was fixed on an experimental run. The data for three observers are shown in Fig. 7.

The data show that the eccentricity of the target affects the time-to-fade (c.f. Ramachandran et al., 1993; De Weerd et al., 1998). As the target gets closer to the fixation point, the time-to-fade increases. The novel result from this experiment is that there is a marked difference in the magnitude of the effect of eccentricity, depending on the type of target employed. DOT targets always take longer to fade than DOM targets and the difference in time-to-fade between the conditions increases as the eccentricity of the target is reduced.

The experiment employed two conditions in which the target was defined by a difference of motion. In one case, the black and white dot pattern within the target was stationary (filled triangles in Fig. 7), in the other it moved with a constant velocity of 2.2 deg s^{-1} (open diamonds). The data obtained in both cases follows a similar pattern, with only small, non-systematic differences between the two conditions. We reserve discussion of this similarity until Section 4.3.

3.3.2. Effects of target size

The previous section provided evidence showing that time-to-fade depends on eccentricity. This result could be related to the decrease in cortical representation

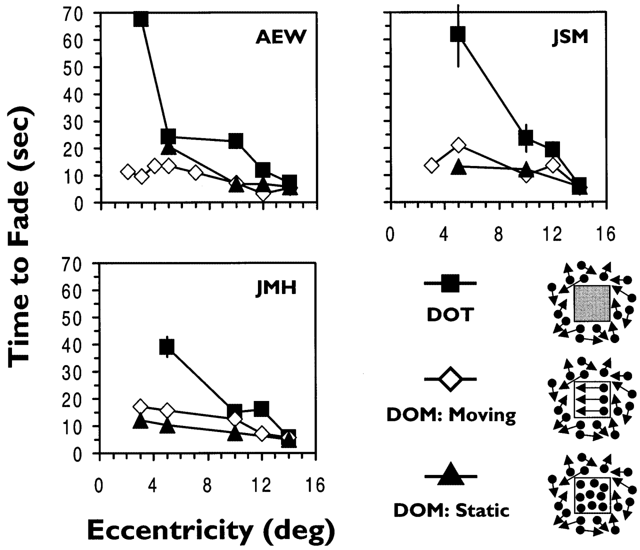

Fig. 7. Time-to-fade plots as a function of eccentricity. The eccentricity of the target reflects the angular distance between the fixation marker and the right hand edge of the target. Curves with black squares represent data for difference of texture (DOT) targets; open diamonds represent data for a target defined by a difference of motion (DOM) containing a random pattern of black and white dots that moved coherently; filled triangles represent data for DOM targets containing a static pattern of random black and white dots. Error bars represent the S.E. of the mean time-to-fade; many lie within the symbols.

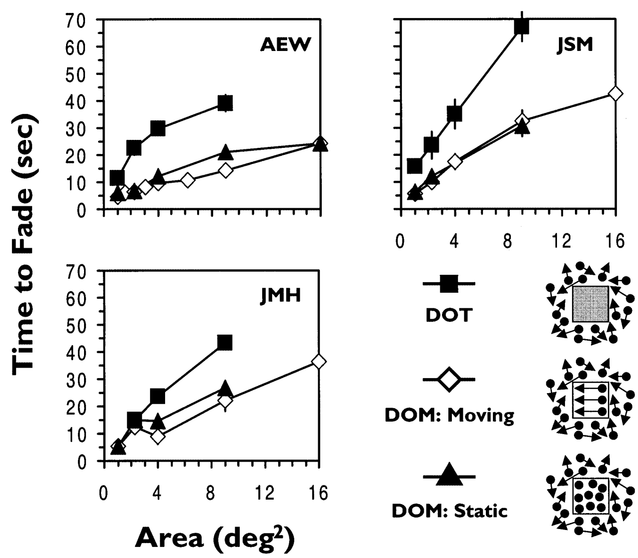

Fig. 8. Time-to-fade plots as a function of target area. Black squares represent data for DOT targets; open diamonds DOM targets containing moving dots; black triangles DOM targets containing static dots. Error bars represent the S.E. of the mean time-to-fade.

(Tootell, Silverman, Switkes, & De Valois (1982) and see De Weerd et al. (1998)) found at larger eccentricities. Next we examined target size, which will also vary the size of the cortical representation of the target. Again, we examined DOT and DOM targets.

The right hand edge of the target was presented at an eccentricity of 10 deg, whilst the size of the target was manipulated by changing side length (see Fig. 1A). Three experimental conditions were used: one DOT and two DOM.

Fig. 8 shows the results of manipulating target size; time-to-fade is plotted as a function of target area. As in the previous experiment, we replicate the finding that time-to-fade increases as the target increases in size (De Weerd et al., 1998). As we observed for changing target eccentricity (see Section 3.3.1), we find DOM targets consistently fade faster than DOT targets of the same size. The gradient of the time-to-fade function is steeper for DOT targets than for DOM targets. Again, we note little difference in the effects on time-to-fade between the DOM static target condition (filled triangles) and the DOM moving target condition (open diamonds) (see Section 4.3 for discussion).

We should note here that the times-to-fade we report are longer than those presented by De Weerd et al. (1998). These differences could be accounted for by differences in the stimulus and the experimental methods employed. In particular, we used dense dynamic random dot patterns for the surrounding texture whereas they employed sparser, dynamic line segments (for evidence of shorter fading times with lower dot densities see Welchman & Harris (2000)). In addition, their stimulus exposure interval was limited to 20 s, whereas here it is under the control of the subject, allowing for times greater than 20 s to be recorded.

4. Discussion

4.1. Physical properties of the target

This paper has examined how the physical properties of a target under the perceptual fading paradigm affect the long-term visibility of that target. This was done to improve our understanding of what might be occurring during the adaptation stage of this perceptual illusion.

In our first experiment, we manipulated the luminance of the target relative to the background and found that this affected the time-to-fade. Introducing luminance contrast between the target and the background causes the time-to-fade to increase. This suggests that the illusion does not simply result from the differences in texture between the target and the surround. Rather, it can be seen as akin to other forms of adaptation, where each aspect of the differences between the two areas must adapt before fading can occur.

Our second experiment enabled us to expand on this basic finding. First, using the Difference of Motion (DOM) stimulus, we showed that increasing contrast across other stimulus dimensions (specifically speed and direction) also elevated the time-to-fade. Second, the DOM stimulus allowed the difference between the target and the background to be defined along the same visual dimension. We were thus able to quantify the visibility of the target. By measuring the subjects' sensitivity to the presence of the target and using it to estimate target visibility, we found that whilst important, visibility did not uniquely specify time-to-fade. The temporal energy of the background dots also appears to be an important factor. The experiment further demonstrated that the perceptual fading of targets is not limited to their being surrounded by dynamic random noise: fading can be obtained when the surround contains coherently moving dots. Why is this interesting? It suggests that perceptual disappearance can occur for stimuli that are potentially more informative than 'unnatural' random noise.

In our third experiment, we observed different time courses for fading when varying the size and the eccentricity of different types of target. Targets defined by a difference of motion faded from view faster than those defined by a difference of texture, and this difference increased as the target got larger in size, or got closer to the fixation point. We discuss the implications of these differences in more detail below.

4.2. 'Contrast' between the target and background

Experiment 3 provided evidence for striking differences in the time-to-fade functions obtained when the target area contained different visual attributes. Why might this be so? Experiment 2 suggested a relationship between target visibility and time-to-fade, so it could be that the DOM targets were simply less visible than their DOT equivalents. Ideally, this suggestion could be evaluated by equating the visibility of DOM and DOT targets and then measuring time-to-fade. However, as the DOT stimulus contains differences between the target and the background that are defined along two visual dimensions (texture and motion) it was not possible to obtain meaningful thresholds for visibility. Varying target properties along one dimension to measure visibility would alter the other, which would change the stimulus.

More generally, we can consider the importance of the contrast between the target and its surrounding texture in determining time-to-fade. Contrast can be described with reference to a number of different visual attributes. For the stimuli we have employed, we regard the differences between the target and the background in luminance, texture, speed and direction as important. Exactly how the visual system combines the different sources of contrast information about the target and the background cannot be determined from our data. For example, motion contrast could combine linearly with luminance contrast, to double the time needed for perceptual fading to occur, but we have no reason to assume that equal weighting would be given to different sources of contrast information. Further, if contrast detection occurs in different cortical locations, then the amount of time taken for the neural fatigue, or gain change, assumed to be important in fading could vary, i.e. different contrast detection mechanisms might have different decay functions. Further experiments will be required to resolve the ambiguity regarding the combination of different sources of contrast information.

4.3. Similarities in behaviour in response to static and moving DOM targets

Experiment 3 employed two types of difference of motion target. In one case, the dots within the target moved with a constant speed, in the other the dots within the target were static. The pattern of results for both types of DOM target was very similar. This is intriguing as the two varieties might be expected to provide the brain with different types of cue. In particular, it might be expected that a stronger positional cue was present when the target dots were static, which might make fading slower than when only motion information is present.

There are three possible reasons for the similarities in the times-to-fade observed with the different DOM targets. First, the motion within the target would be irrelevant if perceptual fading results from a process that is motion-blind. The results of experiment 2 argue strongly against this suggestion. Second, the difference in motion between the target and the background might be sufficiently similar for both types of target to produce a similar pattern of behaviour. In other words, the visual system might treat differences between random motion and zero motion, and random motion and motion of 2.2 deg s^{-1} as being roughly equivalent, thus producing fading over a similar time scale. Last, it might be that different mechanisms are involved in the fading of static and moving DOM targets, but that these mechanisms respond in similar ways. This is also a possibility. Our current data are not able to distinguish between these last two hypotheses. We consider the notion of separate mechanisms for different target types below.

4.4. Different targets — different cortical loci?

An alternative way to think about the differences we observed between the behaviour of subjects with targets defined by different visual attributes is to speculate that different mechanisms are involved in the fading of different types of target. These different mechanisms might have a basis in different neural populations.

It is tempting to draw analogies between the properties of our stimuli and the known properties of neurones in the visual cortex. For example, there is a non-linear anatomical mapping from the retina to striate cortex (Holmes, 1945; Tootell et al., 1982; Van Essen, Newsome, & Maunsell, 1984), such that the fovea is over represented (40% of the area of striate cortex represents the central 5 deg around the fovea). This can be quantified in terms of a cortical magnification factor (Daniel & Whitteridge, 1961). As discussed in detail by De Weerd et al. (1998), the fact that smaller and more eccentric targets fade faster is consistent with fading being related to the amount of cortex that responds to the target. That we observe increases in the time-to-fade with increasing size or decreasing eccentricity of the target (see Figs. 7 and 8) is suggestive of the influence of cortical magnification. However, Figs. 7 and 8 also demonstrate that time-to-fade is very different for DOT and DOM stimuli. Can this result be understood in terms of the underlying cortical physiology and anatomy? We can speculate two possible, but not exclusive, explanations.

First, it is well known that at the level of the lateral geniculate nucleus there are two distinct cell classes (Wiesel & Hubel, 1966). Parvocellular (P) cells have small receptive fields, slow transmission velocities and low contrast sensitivity, whereas magnocellular (M) cells have large receptive fields, fast transmission velocities and high contrast sensitivity. Further, it has been suggested that the cortical mapping varies with eccentricity in different ways for P and M afferents (Schein & DeMonasterio, 1987; Azzopardi, Jones, & Cowey, 1999). The ratio of P to M afferents declines as eccentricity increases, with considerably more P to M afferents for the fovea. DOT and DOM stimuli might differentially activate M and P cells, with DOM stimuli producing more activity in M cells. For example, as M cells have larger receptive fields, the effects of changing the size of the target stimuli or the eccentricity could produce smaller changes in the activity of these neurones than would occur for stimuli producing more activity in P cells. This would be consistent with our results.

Second, we can consider the different patterns of fading in terms of the activation of different cortical areas that may have different cortical magnification factors. De Weerd et al. (1998) applied cortical magnification estimates for the human brain from Sereno, Dale, Reppas et al. (1995) and found a good correspondence between the size of the cortical representation of the target in areas V1 and V3 and the time taken for their target to disappear.[3] This is analogous to the electrophysiological recordings by De Weerd et al. (1995) from awake behaving monkeys viewing a target embedded in dynamic texture. They observed that over a time period similar to that of human perceptual fading, the activity of neurones representing the target increased to the level of the surrounding texture in cortical areas V2 and V3 but not V1.

How pertinent is De Weerd and collegues' (De Weerd et al., 1995, 1998) suggested involvment of area V3 in fading to our study? Area V3 might be involved in the fading of the targets we define as DOT, whereas, the fading of the DOM targets may involve area MT where cells show speed and directional selectivity and typically have larger receptive fields (Maunsell & Van Essen, 1983; Mikami, Newsome, & Wurtz, 1986; Lagae, Raiguel, & Orban, 1993). Alternatively, the fading of DOT and DOM targets may involve a different population of neurones in Striate and extra-Striate cortex. Either way, the expectation would be that the fading of DOM targets involved a mechanism with larger receptive fields than that of DOT targets. This would attenuate the differences in the time-to-fade of DOM presented at different eccentricities and of different sizes, accounting for the pattern of results found in Experiment 3.

4.5. What is responsible for perceptual filling-in?

This paper has addressed factors that impact on the length of time taken for subjects to report that the target is no longer visible. We have shown that perceptual fading is not limited to specific types of target or dynamic random dot backgrounds. In addition, we have quantified how initial target visibility plays a role in determining long-term visibility. However, this work is not directly informative about what is responsible for the outcome of that adaptation — i.e. what it is that causes the perception that there is no target when in fact the target is present in the visual stimulus. Studying the time course of adaptation allows us to quantify the process of perceptual fading. De Weerd et al. (1998) related time-to-fade to the area of cortical projection in areas V1 and V3. The work presented here on differences in motion might also implicate cortical area MT. So, if an active 'neural filling-in' mechanism is to be hypothesised (c.f. Ramachandran & Gregory, 1991; De Weerd et al., 1998), such a mechanism may be active in multiple brain areas, producing fading for different types of target. If competition between the representation of the target and the surround is important (c.f. De Weerd et al.) then this competition might occur in multiple brain areas, according to the particular features of the target. However, the necessity for an active filling-in mechanism is disputed (see Dennett (1991) and O'Regan (1998)). It is possible that observers are no longer aware of the target's presence due to the loss of a neural signal following a sufficient period of adapta-

[3] We would like to have performed similar analysis to compare the cortical projections of our DOT and DOM targets in different cortical areas. Unfortunately, we were unable to find estimates of cortical magnification in human MT.

tion. Future work must more thoroughly examine what happens once the target has disappeared, rather than simply what determines how long it takes to go.

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